A Late Miocene Pipine Frog From The Urumaco Formation, Venezuela

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Abstract: THE PIPIDAE currently hosts about 35 species, with a disjoint Gondwanan distribution that only in the last decades, due to human introduction of the African Xenopus in four continents, expanded into Laurasian countries where this frog is often regarded as a pest (Tinsley et al., 2015). The extant pipid genera can be grouped into two clades, Pipinae and Xenopodinae, whose content varies according to different phylogenetic analyses. The molecular approach favours in most cases the inclusion of the sole Pipa in the Pipinae whereas the Xenopodinae host Xenopus (and, if not considered a synonym of the former, also Silurana) plus the Hymenochirini: Hymenochirus and Pseudhymenochirus (see literature cited in Cannatella, 2015). Conversely, the morphological approach generally suggests the inclusion of Pipa and the Hymenochirini in the Pipinae and Xenopus (plus Silurana) in the Xenopodinae (Gómez, 2016, and literature therein). Pipa is South American whereas both the Hymenochirini and the Xenopodinae are currently exclusive (not considering the above mentioned human introductions) of sub-Saharan Africa (Frost, 2017). The pipid fossil record, rather rich and with a much broader geographic range than that currently shown by extant species (Báez, 1996; Sanchiz, 1998; Gómez, 2016), consists mostly of Cretaceous and Paleogene remains that play a relevant role in the analysis of the earlier history of such disjoint—but at the same time possibly intertwined—distribution. South America hosted several taxa related to the crown Xenopodinae from the Cretaceous to the Late Pleistocene, but no Hymenochirini are recorded there (Gómez, 2016). The South American post-Paleogene record is remarkably scarce and Pipa has virtually no fossil record, except for the mention by Liais (1872) of an entire 'head' from the Pleistocene or Holocene of Rio das Velhas in Brazil (Rio Dal Belhas in Sanchiz, 1998). The material was reported to be identical in size and aspect to Pipa bimaculata (a species name that is currently not valid and not listed among the synonyms of Pipa by Frost, 2017). However, the fossil has not been further described or figured and was simply listed as Pipa sp. by Sanchiz (1998). Here we report on a pipid fossil from Corralito, a late Miocene locality in the Urumaco Basin, Venezuela. The Neogene localities in the Urumaco Basin have so far yielded a large number of marine and continental vertebrates belonging to several major clades (Sánchez-Villagra et al., 2010; Carrillo-Briceño et al., 2015) but amphibians had not been reported to date. Most of the continental taxa retrieved are large sized, some being 'gigantic', such as the crocodilians Gryposuchus and Purussaurus, the turtle Stupendemys and the rodent Phoberomys (among others, Sánchez- Villagra et al., 2010; Scheyer et al., 2013). Prospection in the Urumaco Basin carried out in November 2013 yielded few continental vertebrates of small size, including the single amphibian remain that is here described and discussed. Institutional acronyms: AMNH, American Museum of Natural History, New York; AMU-CURS, Colección de Paleontología de Vertebrados de la Alcaldía de Urumaco, Estado Falcón, Venezuela; MDHC, Massimo Delfino Herpetological Collection deposited at the Department of Earth Sciences, University of Turin, Italy; MLP, Museo de La Plata, La Plata, Argentina; MNHN, Muséum National d'Histoire Naturelle, Paris, France; PIMUZ, Paläontologisches Institut und Museum, Universität Zürich, Switzerland.

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A LATE MIOCENE PIPINE FROG FROM THE URUMACO FORMATION, VENEZUELA

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Key words. *Pipa pipa*. Biogeography. Neogene. Amazon. Urostyle. Sacrum. Fossil.

THE PIPIDAE currently hosts about 35 species, with a disjoint Gondwanan distribution that only in the last decades, due to human introduction of the African *Xenopus* in four continents, expanded into Laurasian countries where this frog is often regarded as a pest (Tinsley *et al.*, 2015). The extant pipid genera can be grouped into two clades, Pipinae and Xenopodinae, whose content varies according to different phylogenetic analyses. The molecular approach favours in most cases the inclusion of the sole *Pipa* in the Pipinae whereas the Xenopodinae host *Xenopus* (and, if not considered a synonym of the former, also *Silurana*) plus the Hymenochirini: *Hymenochirus* and *Pseudhymenochirus* (see literature cited in Cannatella, 2015). Conversely, the morphological approach generally suggests the inclusion of *Pipa* and the Hymenochirini in the Pipinae and *Xenopus* (plus *Silurana*) in the Xenopodinae (Gómez, 2016, and literature therein). *Pipa* is South American whereas both the Hymenochirini and the Xenopodinae are currently exclusive (not considering the above mentioned human introductions) of sub-Saharan Africa (Frost, 2017). The pipid fossil record, rather rich and with a much broader geographic range than that currently shown by extant species (Báez, 1996; Sanchiz, 1998; Gómez, 2016), consists mostly of Cretaceous and Paleogene remains that play a relevant role in the analysis of the earlier history of such disjoint—but at the same time possibly intertwined—distribution. South America hosted several taxa related to the crown Xenopodinae from the Cretaceous to the Late Pleistocene, but no Hymenochirini are recorded there (Gómez, 2016). The South American post-Paleogene record is remarkably scarce and *Pipa* has virtually no fossil record, except for the mention by Liais (1872) of an entire 'head' from the Pleistocene or Holocene of Rio das Velhas in Brazil (Rio Dal Belhas in Sanchiz, 1998). The material was reported to be identical in size and aspect to *Pipa bimaculata* (a species name that is currently not valid and not listed among the synonyms of *Pipa* by Frost, 2017). However, the fossil has not been further described or figured and was simply listed as *Pipa* sp. by Sanchiz (1998).

Here we report on a pipid fossil from Corralito, a late Miocene locality in the Urumaco Basin, Venezuela. The Neogene localities in the Urumaco Basin have so far yielded a large number of marine and continental vertebrates belonging to several major clades (Sánchez-Villagra *et al.*, 2010; Carrillo-Briceño *et al.*, 2015) but amphibians had not been reported to date. Most of the continental taxa retrieved are large sized, some being 'gigantic', such as the crocodilians *Gryposuchus* and *Purussaurus*, the turtle *Stupendemys* and the rodent *Phoberomys* (among others, Sánchez-Villagra *et al.*, 2010; Scheyer *et al.*, 2013). Prospection in the Urumaco Basin carried out in November 2013 yielded few continental vertebrates of small size, including the single amphibian remain that is here described and discussed.

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SYSTEMATIC PALEONTOLOGY

ANURA Fischer von Waldheim, 1813
PIPIDAE Gray, 1825
PIPINAE Gray, 1825

Pipa Laurenti, 1768
cf. ***Pipa*** sp.
Figure 1.1–3

Material. **AMU-CURS**-726: fused sacral vertebra and urostyle.
Locality. Corralito Locality, Urumaco, Falcón State, Venezuela (Scheyer *et al.*, 2013).
Stratigraphy and Age. Lower Member of the Urumaco Formation, late Miocene (Quiroz and Jaramillo, 2010).
Description. The preserved portion of the fused sacrum and urostyle is 25.2 mm long (Fig. 1.1–3). The compound element is incomplete and its bone surface is moderately to strongly damaged. However, the characters listed below are clearly present: 1) laminar and anteroposteriorly distally expanded sacral diapophyses developed on a rather horizontal surface and laterally incomplete (maximum width of the preserved portion is 14.6 mm); 2) sacral sagittal dorsal ridge, the neural crest, merging posteriorly with the dorsal crest (crista dorsalis) of the urostyle; 3) sacral centrum ventrally flat and rather broad; 4) neural canal of the sacral vertebra relatively small; 5) presence of a broad spinal foramen on each side of the fossil, below the expanded diapophyses. The dorsal surface of each sacral diapophysis has the remnants of a ridge placed close to the posteromedial edge of the bone; the two ridges are rather symmetric and diverge from each other at an angle of about 90°. The shapes of the articular surfaces of the sacral prezygapophyses as well as that of the sacral centrum cannot be evaluated with confidence.
Identification. Despite the poor preservation of AMU-CURS-726 several characters are available and useful for its identification. The fact that the sacrum and the urostyle are fused to each other might indicate referral to the Pipidae, although this character occurs in other American taxa, such as some pelobatoids (Cannatella and Trueb, 1988a,b; Báez and Trueb, 1997) and some bufonids (*e.g.*, Cannatella, 1986; Chaparro *et al.*, 2007; Páez-Moscoso *et al.*, 2011). In the only living American pelobatoids, the Scaphiopodidae, the expanded sacral diapophyses do not bear ridges on the dorsal surface, close to their posteromedial edges, as shown for example by *Scaphiopus holbrooki* (AMNH A-16603, A-58186) and *Spea multiplicata* (AMNH A-56289, A-62560, A-177074, A-177075), whose diapophyses are clearly tilted dorsally and not nearly perpendicular with respect to the sagittal plane of the skeletal element as in AMU-CURS-726. Therefore, pelobatoids can be excluded on a morphological basis and not only for biogeographic reasons. The sacral morphology of most Neotropical bufonids has not been described in detail, but at least the sacral diapophyses of two species with fused sacrum and urostyle are dorsally devoid of a ridge close to the posteromedial edge (Chaparro *et al.*, 2007; Páez-Moscoso *et al.*, 2011) and hence clearly not congruent with AMU-CURS-726.

Among pipids, the presence of a neural crest on the sacral vertebra allows us to exclude the Xenopodinae (Cannatella and Trueb, 1988a; occasionally present in *Xenopus* according to Báez *et al.*, 2008), limiting the options to the Pipinae. Many members of Pipinae have a sacral neural crest: it is present in *Hymenochirus* and *Pseudhymenochirus* (Cannatella and Trueb, 1988b) and at least in most *Pipa* species (where it is variably present according to Báez *et al.*, 2008). Moreover, the presence of a scar, interpreted here as evidence for the former occurrence of a posteromedial ridge on the dorsal surface of each sacral diapophysis of AMU-CURS-726, excludes its referral to *Hymenochirus* and *Pseudhymenochirus* (Cannatella and Trueb, 1988b: fig. 3) and further confirms the exclusion of *Xenopus* (*Xenopus laevis* AMNH A-72534, A-177084, A-177085, A-177086, A-177087; including *Silurana*, see Báez *et al.*, 2008: fig. 3D). The presence of this character among the seven species of *Pipa* is not universal. It seems to be consistently present in *Pipa pipa* (AMNH A-51645, A-57989, A-58443; MDHC 440; MNHN 1882-461; Fig. 1.4,5), but absent in *Pipa arrabali* (AMNH A-51175), *Pipa aspera* (see Trueb and Massemin, 2001: fig. 4B, but the drawing might be too schematic to show the sacral

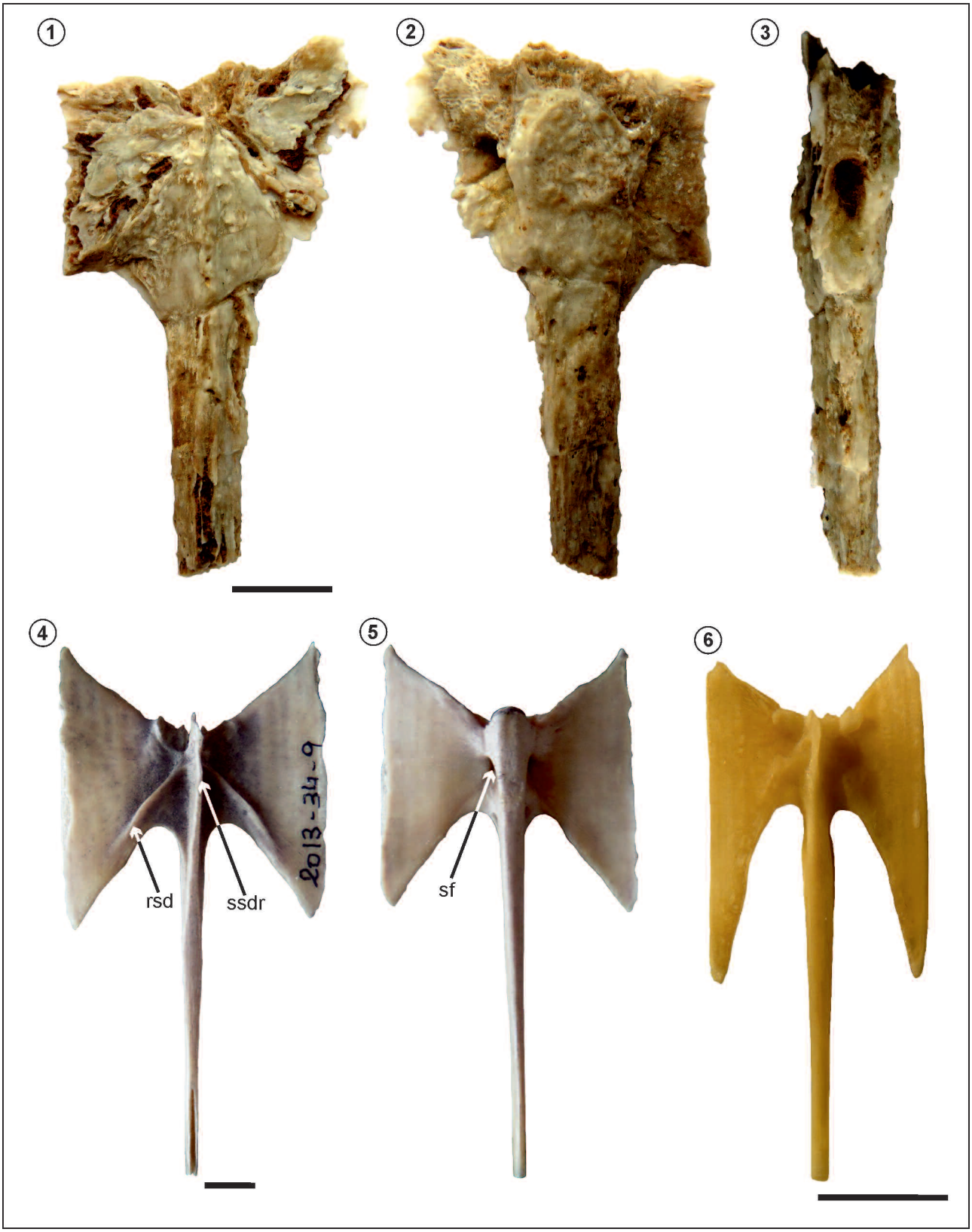

Figure 1. 1–3, cf. *Pipa* sp. AMU-CURS-726 from the late Miocene of Corralito (Urumaco Basin), fused sacrum and urostyle in dorsal, ventral, and right lateral views; **4–5, *Pipa pipa* MNHN 1882-461,** fused sacrum and urostyle in dorsal and ventral views; **6, *Pipa parva* PIMUZ A/II 118,** fused sacrum and urostyle in dorsal and ventral views. Abbreviations: **rsd**, ridge on sacral diapophysis; **ssdr,** sacral sagittal dorsal ridge; **sf,** spinal foramen. Scale bars= 5 mm.

ridges), *Pipa carvalhoi* (Báez *et al.*, 2008: fig. 3F), *Pipa myersi* (Trueb, 1984: fig. 5) and *Pipa parva* (Fig. 1.6; PIMUZ A/II 118; Báez *et al.*, 2008: fig. 3E). Samples of *Pipa snethlageae* were not available for this study and apparently not described or figured in the literature. As for the extinct pipids from South America, analogous ridges occur in *Shelania pascuali* from the Eocene of Patagonia, which is currently considered a Xenopodinae (Estes, 1975; Báez and Trueb, 1997; Báez *et al.*, 2008; Gómez, 2016). This taxon, however, is characterized by the absence of a mid-dorsal crest (see for example Báez *et al.*, 2008: fig. 3C) unlike AMU-CURS-726 and thus they do not represent the same taxon.

For the sake of completeness, AMU-CURS-726 can also be compared with the only post-Paleogene fossil pipids described from South America, from the Pleistocene of Argentina (Báez *et al.*, 2008, 2012). The material from Daireaux consists of a single ilium referred to a stem Xenopodinae, but the one from Centinela del Mar includes MLP 04-V-2-220, an incomplete sacrum fused with the urostyle whose identification and relationships are still to be determined based on additional material because of the incongruent suite of characters (Báez *et al.*, 2008). However, the ridge on the sacral diapophyses are not described nor evident in the available drawing of MLP 04-V-2-220 (Báez *et al.*, 2008: fig. 3A).

Because of the presence of a mid-dorsal crest and ridges on the diapophyses, the pipid from Corralito is therefore referred to *Pipa* (as cf. *Pipa* sp.), pending the discovery of additional material from the same locality that might help to evaluate its phylogenetic relationships.

It is not possible to analyze the relationships of AMU-CURS-726 because even if the characters currently applied to explore the phylogenetic relationships among the extinct and extant pipids are highly detailed and numerous, very few of them refer to the sacrum-urostlyle complex (9 out of 165 characters used by Gómez, 2016) and most of them cannot be evaluated on AMU-CURS-726 because of its poor preservation.

DISCUSSION AND CONCLUSIONS

Recent investigations indicate that crown-group pipids were already diversified into three lineages by the Late Cretaceous (Cannatella, 2015; Gómez, 2016), but the contribution of palaeontology to the evolutionary history of the South American *Pipa* is virtually null, since the only fossils putatively referred to this genus come from an undetermined Quaternary of Brasil and were reported (not figured or described) as identical to that of extant *Pipa* (Liais, 1872). This is quite surprising for a clade of anurans that is morphologically highly derived, with a well-known osteology (*e.g.*, Trueb *et al.*, 2000) and that is therefore potentially easily identifiable.

The material from the late Miocene of northern Venezuela here referred to *Pipa*, besides being the first land microvertebrate reported for the Urumaco Formation, contributes to partly fill the gap of the South American pipinae. Being represented by a single, poorly-preserved skeletal element, its bearing on the evolutionary history of this clade is currently minimal, but testifies that the Urumaco Basin could potentially provide more informative remains.

Pipa currently inhabits Venezuela and even the State of Falcón with the species *Pipa parva* (Mijares-Urrutia and Arends, 2000). AMU-CURS-726 is not referable to *Pipa parva* primarily because the latter lacks the ridge on the sacral diapophyses, but also because this taxon has, as indicated by its name, a small size, whereas the size and the few available characters of the fossil from Corralito are consistent with *Pipa pipa*. At present, the latter has a broad range in the Amazon Basin, including Venezuela (IUCN SSC Amphibian Specialist Group, 2015), but not in the now arid region of the Sate of Falcón where the Urumaco Basin is located. However, as summarized by Scheyer *et al.* (2013, p. 7), "[*palaeoenvironmental reconstructions based on palynofloras from the Urumaco Formation suggest a continuation of the Amazonian forest into northwestern Venezuela during the Miocene, with the faunal context including marginal marine, freshwater and continental vertebrates*]". The possible presence of large-sized *Pipa* in the Urumaco Basin could represent a further evidence of such relationship with the Amazonian Basin, before tectonic events leading to the uplift of northern Andes and consequently changes in the course of rivers, as well as climatic changes, disrupted such relationship (Hoorn *et al.*, 2010; Pimiento *et al.*, 2017).

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